

Age and growth analyses for the endangered belugas in Cook Inlet, Alaska

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Belugas, *Delphinapterus leucas*, Pallas (1776) are toothed whales of the Monodontidae family which includes only one other species, the narwhal, *Monodon monoceros*. Belugas are circumpolar in distribution and occur only in the Northern Hemisphere, in seasonally ice-covered seas of temperate, subarctic, and arctic regions. Belugas in U.S. waters surrounding Alaska are managed by the National Marine Fisheries Service (NMFS) as five discrete stocks designated by their summering areas (Muto et al., 2018). The Cook Inlet stock is genetically distinct (O'Corry-Crowe, Suydam, Rosenberg, Frost, & Dizon, 1997) and geographically isolated from the other stocks (Lowry, O'Corry-Crowe, & Goodman, 2012).

The geographic isolation of these whales, in combination with their site fidelity (Shelden et al., 2015), makes this stock vulnerable to hunting (Mahoney & Shelden, 2000) and other anthropogenic impacts (Norman et al., 2015). The Cook Inlet beluga (hereafter CIB) population is listed as endangered under the U.S. Endangered Species Act and critically endangered on the IUCN Red List (Lowry et al., 2012; NAMMCO, 2018). As the population continues to decline (Hobbs, Shelden, Rugh, Sims, & Waite, 2015a), the lack of basic life-history information has hampered attempts to determine causes (Hobbs, Wade, & Shelden, 2015b). In particular, knowing the ages of animals in this population is key to further demographic study.

Vos (2003) estimated ages of CIBs by reading growth layer groups (GLGs) in the thin sections of teeth that were collected from hunted and stranded belugas during the period 1992–2001. Herein, we include data from this earlier study, and with additional teeth collected up to June 2015, present results validating the number of GLGs deposited in the tooth dentine each year. We compared ages obtained from each mandible and from the anterior to the posterior of the mandible to determine the “best” tooth for aging. We then compared length-at-age models for CIBs.

Tooth collection procedures were dependent on when the teeth were collected (protocols changed through the years to include collection of the entire mandible when possible), the length of time the whale was dead, the whale's position on the ground, who collected the teeth, and the physical location of the carcass. Most teeth were collected by

removing one or both mandibles from dead whales (hunted or stranded) reported to the Alaska stranding network. However, in some instances only individual teeth were collected. Teeth were collected from 108 belugas necropsied between September 1992 and June 2015 (Table S1). Length measurements from calves-of-the-year ($n = 10$) and one full-term fetus provided a starting point for the length-at-age models. Collection location was reported for 117 whales (often a descriptive location not a latitude/longitude), with most coming from the Susitna River delta ($n = 32$) and the Anchorage area ($n = 32$) (Figure 1).

Genetic analysis and/or field observations were used to determine sex. The sexes were evenly represented, 55 females and 57 males. We were unable to find matches in the genetics database for an additional seven whales

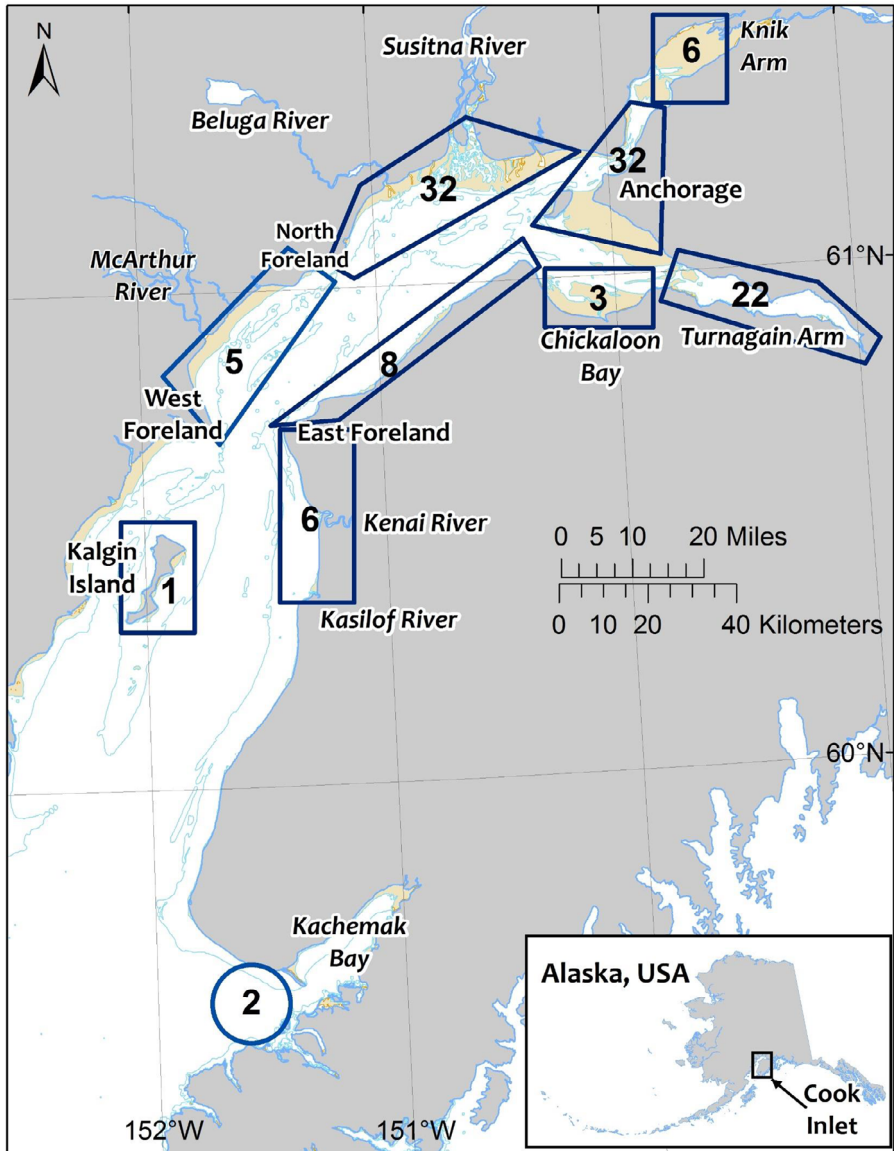


FIGURE 1 Regions within Cook Inlet, Alaska, where tooth samples were collected from deceased belugas during the period September 1992–June 2015. The numbers indicate how many whales were sampled within each region (note: descriptive locations were often provided not latitude/longitude, see Table S1 for dates, regions, number of teeth aged, and morphological data).

of unknown sex (Table S1). Whale body length was measured to the nearest cm from the tip of the rostrum to the fork of the fluke with the tape measure stretched in a straight line. Length measurements for 19 whales (8 females, 4 males, and 7 of unknown sex) were not collected or were estimated (e.g., due to missing flukes), and, therefore, could not be used in the length-at-age models. Subsistence hunters usually removed the flukes immediately after landing a whale (Mahoney & Shelden, 2000). Hunted whales comprised 15% of the sample (17 females, 16 males). Subsistence hunting has not been authorized since 2006, and most of the hunted whales in the tooth-aging sample were from the period 1993–1998 (Table S1). Hunted whales were primarily from the Susitna River delta area (24 of the 34 whales, Figure 1). Captures and tagging of belugas in Cook Inlet took place from 1999 to 2002 (Ferrero, Moore, & Hobbs, 2000; Shelden et al., 2018). Although teeth were not collected at the time of capture, teeth from two tagged male belugas that stranded and died in 2014 and 2015 provided ages that support recent findings on dentine deposition rates (presented below).

Beluga teeth are simple, peg-like structures that have single roots and are deeply embedded in the alveoli of the jaws (Stewart & Stewart, 2014). Mandibular teeth were used for aging, primarily due to the ease of taking the lower jaw. Teeth were numbered from 1 to 10 on each mandible, starting at the anterior tooth and ending at the posterior tooth (Figure 2).

Mandibles were heated in water until the teeth loosened and could be removed from the jaw. Depending on the number of teeth collected, analysts estimated ages from 1 to 20 teeth from each whale (Table S1). Teeth were cleaned and mounted on wooden blocks with hot glue or epoxy. Longitudinal midlines were drawn on each tooth to show the best plane for cutting and sectioning. The blocks holding the teeth were held with a machine vice with a micrometer adjustment. Each tooth was cut into thin sections between 0.30 mm and 0.50 mm thick using either a Felker saw, a Sherline milling machine, or a Buehler Isomet saw. All saws were equipped with diamond-impregnated, lapidary blades that were cooled with water. These methods follow similar standards detailed in Vos (2003) and Lockyer, Hohn, Hobbs, and Stewart (2016).

Two analysts estimated ages independently. Tooth sections were viewed wet or dry, on a dissecting microscope using transmitted and/or reflected light. The choice in light depended on the analyst and the individual tooth. The analysts were not provided any information about the whale such as length, sex, or location of the tooth in the mandible. Each analyst independently recorded the number of GLGs, presence or absence of a prenatal cap, and any comments on readability. A GLG was defined as a combination of one dark and one translucent layer in the dentine of the tooth as standardized in other studies (Read, Hohn, & Lockyer, 2018; Vos, 2003). Belugas only have one set of teeth in their lifetime, as with other odontocetes (Read et al., 2018), and GLGs wear away over time. A prenatal dentine cap at the tip of the tooth is the first layer to wear away. It is deposited before birth and the dentine is

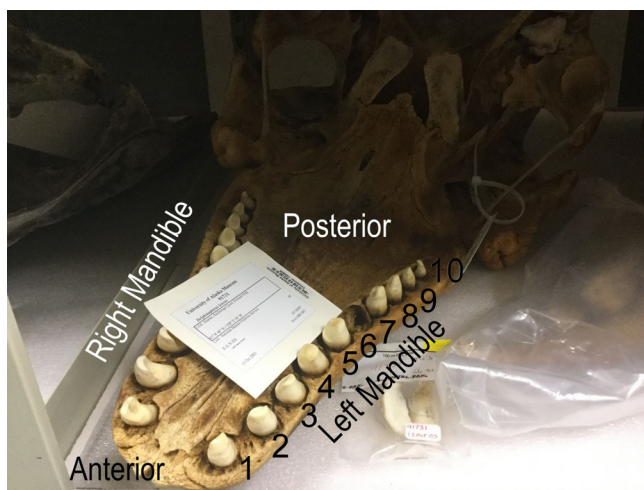


FIGURE 2 Example of the lower mandibles and tooth positions for Cook Inlet belugas. Belugas may have as many as 10 teeth per mandible, but often have eight teeth (photo of Whale ID #80 [see Tables S1 and S2] courtesy of UAF-UAM).

homogenous with no GLGs as compared to postnatal tooth growth (Read et al., 2018). If a worn tooth (no prenatal layer) ended in a partial GLG, the age was rounded up to include that portion as a GLG (Lockyer et al., 2016). Beluga ages are reported as minimums unless the prenatal cap was present indicating that no growth layers had worn away (see example teeth in Figures S1–S3).

Readability was defined by the precision of counting GLGs. For an excellent tooth, the analyst could achieve the same GLG count with no discrepancies among counts. A good or fair tooth would yield a one or two GLG variation in counts, but the analyst could confidently decide on a final age. Unreadable teeth gave results that varied by more than three GLGs. After teeth were independently examined, the analysts compared their recorded ages. Any differences were resolved by both analysts cooperatively reexamining the tooth, agreeing upon a final age, and sometimes looking at other teeth from the same animal. The age selected for each beluga was the maximum GLG count regardless of tooth position.

Recent studies concluded one GLG rather than two GLGs are deposited yearly in beluga teeth (Hohn, Lockyer, & Acquarone, 2016; Lockyer et al., 2016; Matthews & Ferguson, 2014; Read et al., 2018; Waugh, Suydam, Ortiz, & Thewissen, 2018). Based on those results and findings from this study, we assume that each GLG represents one year of age for CIBs. Our independent validation of GLG deposition rate is based on analysis of the teeth collected from two whales that were satellite tagged in 2002, and stranded and died in 2014 and 2015, respectively (Shelden et al., 2018). The younger animal (CI-0205, ID #115; Table S1, Figure S2) had teeth aged at 20 GLGs at the time it died in 2015. This beluga would not have been born at the time of tagging if two GLGs deposited per year. Instead, a minimum age of 7 (note: no teeth had prenatal caps) appears appropriate for this whale (Figure 3), which was described at the time of tagging as a “white-gray beluga” measuring roughly 386 cm in length (Shelden et al., 2018). Similarly, CI-0208 was 23 GLGs at the time it died in 2014 (ID #110, Table S1), placing this beluga at a minimum of 11 years old at the time of tagging when it was described as “white-gray” in color and roughly 376 cm in length (Shelden et al., 2018).

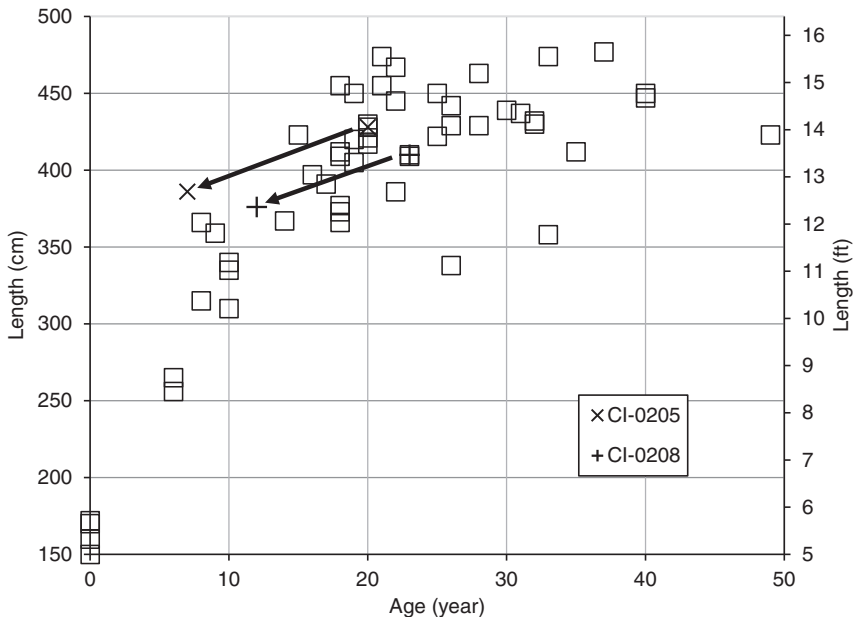


FIGURE 3 Length and age at capture and at death for two male belugas tagged in Cook Inlet, Alaska, August 2002. Arrows point to the length-at-capture and calculated age (assuming one GLG per year) with comparison to lengths and ages of all other males (square symbols) in the tooth aging sample.

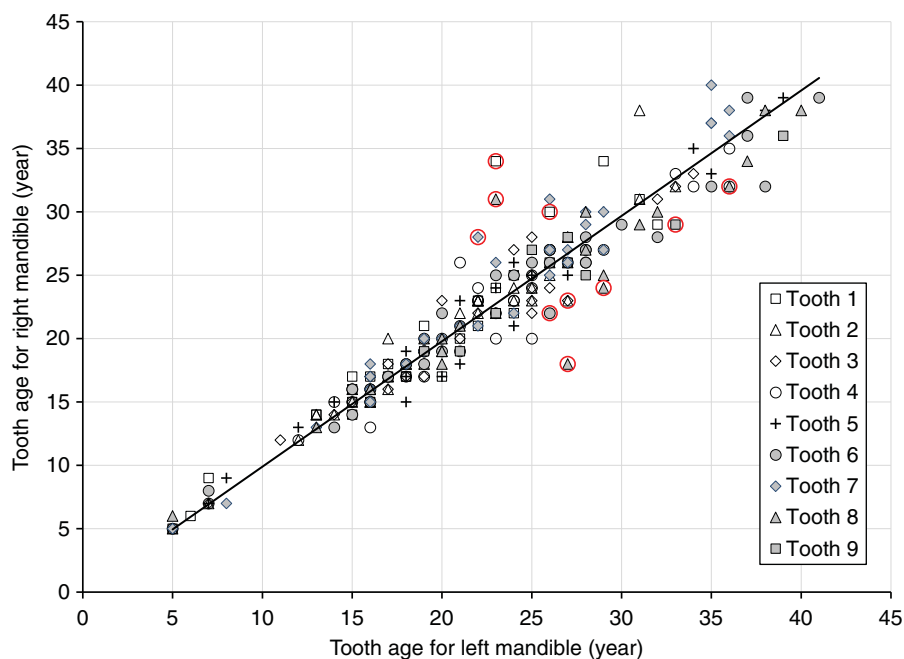


FIGURE 4 Ages of paired teeth between right and left mandibles of belugas from Cook Inlet, Alaska (linear regression line $R^2 = 0.93$, $y = 0.99x$). Pairs with one “unreadable” tooth ($n = 10$) are shown within red circles.

To determine if ages varied between jawbones, we compared ages from pairs of teeth across mandibles. Forty-six whales had left and right mandibles with at least one matched pair (274 pairs total) among the tooth positions. We included all pairs in the analysis but note that for 10 of the pairs, one thin section was classified as “unreadable” (Figure 4, red circles; also see example in Figure S3). Overall, ages obtained from each mandible were similar, 72% of paired teeth were within 0 to ± 1 year, and 86% within ± 2 years ($R^2 = 0.93$). Therefore, teeth from either mandible may be used when determining age, however, the location of the tooth within the mandible did affect age.

For 93 whales, the teeth collected were of known position in the mandible (Table 1). Loss of prenatal caps became evident by age 9. The oldest male with a prenatal cap was 18, while the oldest female was 31 (Table 1). Prenatal caps were present on 8% of the 899 known-position teeth examined (Tables 2, S1, Figure S1). The highest percentages of prenatal caps were found in teeth 6–9 in the posterior portion of the lower mandible (Table 2). This suggests that teeth selected for aging should be posterior of tooth 5. However, if the prenatal cap has worn away, we also needed to test whether the anterior teeth continued to wear down more than the posterior teeth.

We compared the average age for tooth positions 1–5 to the average age for tooth positions 6–9 for mandibles with at least one tooth aged in both categories ($n = 55$ right mandibles, 60 left mandibles). Older ages were obtained from teeth posterior (6–9) for most mandibles (91%, $n = 105$) (Figure 5). Overall, average ages from posterior teeth were 2.3 years older ($SE = 0.2$, $n = 115$, range: -2.3 – 8.0 years). Comparing ages for whales with at least one mandible containing all posterior teeth 6–8 (54 whales, $n = 36$ right mandibles, 37 left mandibles; see Table S2), we found these teeth represented 84% of the final ages. Tooth 8 and tooth 9 (when present), provided the oldest ages (i.e., final age) most often (33%–62% of mandibles) compared to tooth 6 and 7 (14%–25%), though it should be noted that sometimes multiple teeth matched the final age (Table S2). Only five right mandibles had final ages that came from teeth other than positions 6–9 (Table S2).

A sex-specific length-at-age relationship for CIBs was suggested when examining scatter plots of the data set. Growth curves were created using both the von Bertalanffy (length = $L_{\infty} * \{1 - \exp[-\kappa * (\text{age} - t_0)]\}$) and the Ricker formulation of the Gompertz (length = $L_{\infty} * \exp[-\exp[-g_i * (\text{age} - t_i)]]$) growth-curve models (Hillborn & Walters,

TABLE 1 Number of Cook Inlet belugas with final ages, categorized by presence of prenatal cap, whether tooth position was known, and sex. Whales excluded from the sex-specific age-at-length analysis are shown as U (unknown length or sex) or with an “e” (estimated) after the length measurement (see Table S1). Not shown are 10 calves-of-the-year and one full-term fetus.

Final age	Prenatal cap present (N/Y)						Tooth position known (N/Y)						Grand total
	N			Y			N			Y			
	F	M	U	F	M	U	F	M	F	M	F	M	
2											1		1
4											1		1
6												2	2
8												2	2
9						1						1	2
10											1	1	2
11												1	1
14												1	2
15												1	1
16												1	5
17												1	4
18												1	8
19												3	5
20												4	7
21												1	3
22												2	9
23												6	9
25												2	2

(Continues)

TABLE 1 (Continued)

Final age	Prenatal cap present (N/Y)						Tooth position known (N/Y)						Grand total
	N			Y			N			Y			
	Tooth position known (N/Y)			Sex			Tooth position known (N/Y)			Sex			
	F	M	U	F	M	U	F	M	U	F	M	U	
26				2		3							5
27				1									1
28				3	2	1							6
29				4									4
30				2		1							3
31					1								2
32		1		1									3
33	1	1	1			1							4
35													1
36									1				1
37	1			1		1							3
39				1									1
40						2							2
41				1									1
47				1									1
49						1							1
Grand total	3	7	2	38	35	5	2	1	1	6	9		108

TABLE 2 Number of prenatal caps present for each tooth position for all known-position teeth for 93 belugas necropsied in Cook Inlet, Alaska, 1992–2015.

Number of:	Tooth position										Total
	1	2	3	4	5	6	7	8	9	10	
Prenatal caps	5	7	5	7	8	11	13	13	5	0	74
Teeth	97	118	113	115	125	107	101	85	35	3	899
Caps/Teeth	5%	6%	4%	6%	6%	10%	13%	15%	14%	0%	8%

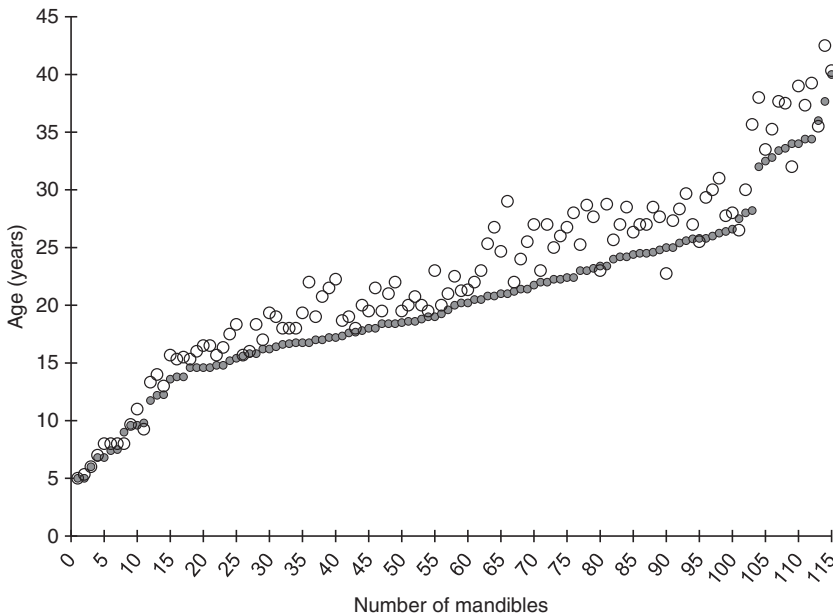


FIGURE 5 Average ages for teeth anterior (positions 1–5) (small, gray circles) and posterior (positions 6–9) (open circles) on the mandible ($n = 55$ right mandibles and 60 left mandibles). Mandibles on the x-axis are organized from youngest average age to oldest based on average anterior age (teeth positions 1–5).

1992; Quinn & Deriso, 1999) using the FSA (Ogle, 2016) analysis package in R (Pinheiro Bates, DebRoy, Sarkar, & R Core Team, 2017; R Core Team, 2016). To compare growth curves for females and males and determine which parameters are sex-specific, a series of eight model parameterizations for each of the two functional forms were fit using the nonlinear least squares estimation (Ogle, 2016). The eight parameterizations were a general model with separate parameter estimates for males and females, three models with one parameter in common between males and females, three models with two parameters in common between males and females, and a common model with the same parameter estimates for both males and females. This resulted in 16 models (Appendix); eight for each model formulation. Models were compared using Akaike's information criterion (AIC) (Burnham & Anderson, 2002) to determine which model formulation and which parameterization best fit the data. Models with $\Delta\text{AIC} \leq 2$ are considered equally well fit. Residuals were examined to confirm that the assumptions for the statistical test were met (Appendix). Residual degrees of freedom and standard error of the estimates are also presented (Table 3).

Growth curves were developed using data from 100 whales with known lengths, 47 females and 53 males. The Gompertz growth-curve model with sex-specific asymptotic length and common shape parameters was the best-fit model (Table 3). Six other models received similar support ($\Delta\text{AIC} \leq 2$): three Gompertz and three von Bertalanffy, all

TABLE 3 Cook Inlet beluga growth curve parameters and results for the seven best-fit models ($\Delta\text{AIC} \leq 2$). Gom = Ricker formulation of the Gompertz growth-curve model. LVB = von Bertalanffy growth-curve model. L_{∞} = asymptotic length, Rdf = residual degrees of freedom, SE = standard error of the estimate, and ΔAIC = difference between the Akaike's information criterion (AIC) for a given model and the minimum AIC value for the set of models. The curvature parameter for the Gompertz model is g_i (instantaneous growth rate at the inflection point) and for the von Bertalanffy model is κ (the Brody growth parameter governing the speed at which L_{∞} is approached). The location parameter for the Gompertz model is t_i (the age at the inflection point) and for the von Bertalanffy model is t_0 (the age when the average length is zero).

Model	L_{∞} (SE)	Curvature (SE)	Location (SE)	Rdf	SE	ΔAIC
Gom: $L_{\infty F}$, $L_{\infty M}$, g_i , t_i	$L_{\infty F} = 383.46$ (5.57) $L_{\infty M} = 438.09$ (6.53)	$g_i = 0.141$ (0.012)	$t_i = -0.173$ (0.360)	96	26.63	0.00
Gom: $L_{\infty F}$, $L_{\infty M}$, g_i , t_{iF} , t_{iM}	$L_{\infty F} = 380.60$ (5.59) $L_{\infty M} = 438.53$ (6.49)	$g_i = 0.145$ (0.013)	$t_{iF} = -0.657$ (0.518) $t_{iM} = 0.255$ (0.460)	95	26.53	0.22
LVB: $L_{\infty F}$, $L_{\infty M}$, κ , t_0	$L_{\infty F} = 388.59$ (6.47) $L_{\infty M} = 443.17$ (7.65)	$\kappa = 0.108$ (0.011)	$t_0 = -4.25$ (0.52)	96	26.70	0.55
LVB: $L_{\infty F}$, $L_{\infty M}$, κ , t_{0F} , t_{0M}	$L_{\infty F} = 386.14$ (6.38) $L_{\infty M} = 443.84$ (7.61)	$\kappa = 0.110$ (0.011)	$t_{0F} = -4.56$ (0.59) $t_{0M} = -3.84$ (0.56)	95	26.69	0.73
Gom: $L_{\infty F}$, $L_{\infty M}$, g_{iF} , g_{iM} , t_{iF} , t_{iM}	$L_{\infty F} = 388.30$ (9.75) $L_{\infty M} = 436.55$ (6.69)	$g_{iF} = 0.122$ (0.020) $g_{iM} = 0.151$ (0.015)	$t_{iF} = -0.756$ (0.613) $t_{iM} = 0.324$ (0.451)	94	26.53	1.16
Gom: $L_{\infty F}$, $L_{\infty M}$, g_{iF} , g_{iM} , t_i	$L_{\infty F} = 390.54$ (9.69) $L_{\infty M} = 436.36$ (6.92)	$g_{iF} = 0.123$ (0.019) $g_{iM} = 0.146$ (0.015)	$t_i = -0.101$ (0.375)	95	26.67	1.32
LVB: $L_{\infty F}$, $L_{\infty M}$, κ_F , κ_M , t_0	$L_{\infty F} = 383.42$ (7.59) $L_{\infty M} = 444.59$ (8.11)	$\kappa_F = 0.119$ (0.017) $\kappa_M = 0.107$ (0.011)	$t_0 = -4.09$ (0.53)	95	26.74	1.78

with sex-specific asymptotic length but different combinations of sex-specific and/or common shape parameters (Figure 6).

All of the best-fit models included sex-specific asymptotic lengths with CIB males reaching a longer asymptotic length than females (Table 3). Models that included sex-specific asymptotic lengths had smaller standard errors ($SE = 26.53$ – 26.74) than models with a single asymptotic length ($SE = 27.42$ – 35.98), suggesting the sex-specific sample more accurately reflects the true overall population (Appendix). The asymptotic length from the best-fit model (rounded to the nearest centimeter) for males was 438 cm (95% CI: 425–451 cm) and for females was 384 cm (95% CI: 372–395 cm); these parameters were similar across the six other supported models. Suydam (2009) presented growth curves and asymptotic lengths for Alaska belugas from the Chukchi Sea, Kotzebue Sound, Cook Inlet, and Bristol Bay. Beluga asymptotic lengths tended to be smaller than what we present here for females in all of these areas and for males in Bristol Bay. However, sample sizes presented in Suydam (2009) were small for Cook Inlet and Bristol Bay. For Cook Inlet, the beluga asymptotic lengths presented by Suydam (2009) were 432 cm (95% CI: 401–461) and 361 cm (95% CI: 351–370) for males ($n = 28$) and females ($n = 17$), respectively. This sample (obtained from Vos 2003, D. Vos unpublished data) lacked young males (<8 GLGs) and young females (2–16 GLGs) resulting in overlap of the male and female growth curves, which has been resolved with the sample analyzed in this paper (Figure 6). The larger size of CIB females we present here remained within the range of asymptotic lengths for all females presented in Suydam (2009), which also included Russian, Canadian, and Greenland populations. These sizes are now closer to females from West Greenland (386 cm, 95% CI: 374–398; Heide-Jørgensen & Teilmann,

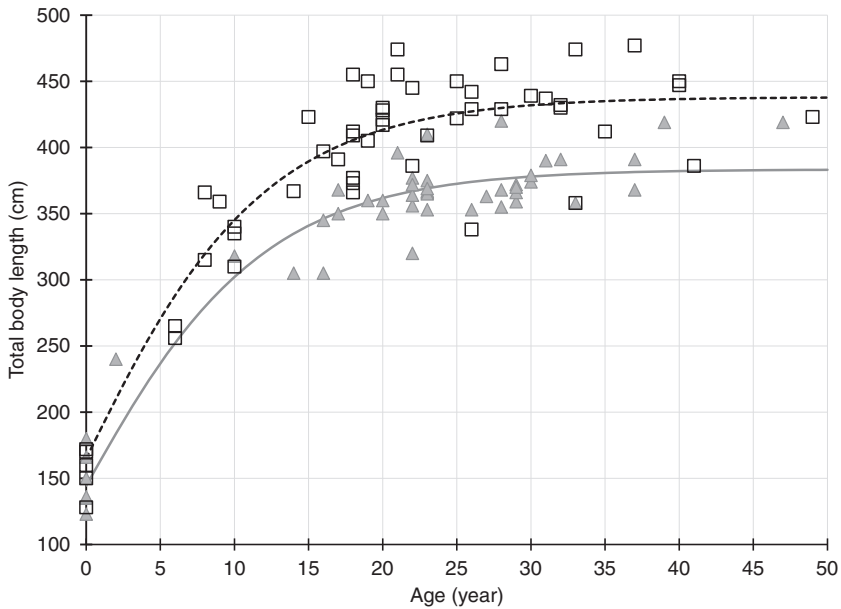


FIGURE 6 Age vs. length plot with best-fit Gompertz growth curves for male (squares and dashed line) and female (triangles and solid line) Cook Inlet belugas.

1994), and the Canadian western Arctic-Beaufort Sea populations (386 cm, 95% CI: 377–395; Harwood, Norton, Day, & Hall, 2002).

The relationship between age and growth is a fundamental parameter of population dynamics. The age at first calving and the age of senescence is needed for realistic modeling of population growth. Our sample included 10 pregnant females ranging in age from 14 to 41 and further analyses of reproductive status for CIBs are planned.¹ In particular, the fact that CIBs deposit one GLG per year has ramifications for studies on fecundity, age of sexual maturity, and accumulation of contaminants.

Growth curves indicated sexual dimorphism, with males larger at asymptotic length. Currently, the sample includes few whales in the youngest and oldest age groups (i.e., under 10 years old and over 40 years old). Increased sample size, particularly in these age categories, would improve the growth curve analysis and help to elucidate whether the shape of the growth curves exhibit sexual dimorphism as well as the asymptotic lengths.

Teeth selected for aging should come from the posterior of the jaw because those teeth exhibit the least amount of wear, greatest frequency of prenatal caps, and the highest GLG counts (e.g., Lockyer et al., 2016; Vos 2003). Belugas typically grasp and swallow prey whole such as salmonids and flatfish (Quakenbush et al., 2015; Rouse, Burek-Huntington, & Shelden, 2017) which may result in greater wear of the anterior teeth. Because tooth wear can be a problem, particularly in older whales, we recommend at a minimum selecting tooth 8 and, if present, tooth 9 for aging. Teeth can be selected from either right or left mandible given similar ages between sides.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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